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Two remarkable Discomycetes

EDWARD T. HARPER

(WITH PLATES 1–3)

1. UNDERWOODIA COLUMNARIS Peck

I have collected this rare plant in several localities in Michigan and Illinois. The first collection was on Neebish Island, Michigan, in August, 1897. A cluster of small plants about two inches high were found growing beside a path in balsam woods. The next year some larger plants were found growing among dead leaves in a ravine on Mackinac Island. In September three different collections were made on Neebish Island, and the photographs on PLATE 1 were taken. In May, 1908, the two plants shown on PLATE 2 were found on a hillside in open woods at Bureau, Illinois. A single plant was found at Neebish during the past summer.

The species was described and illustrated by Dr. Peck in the 43d Report of the New York State Museum, p. 78, *pl. 4* (1890), from plants found near Kirksville, New York, and sent to Dr. Peck by Professor Underwood. A note in Underwood's Moulds, Mildews and Mushrooms, p. 65 (1899), says that six plants were found in the same locality in three different years. Peck's description is accurate as far as it goes, but his account of the base and method of branching of the plant is incomplete. The plant is so unique in structure and so remarkable in habit and size that I have thought it worth while to discuss its structure and relationships on the basis of my specimens.

Peck's illustration shows the part above the ground only, and he describes it as stemless and everywhere acigerous. This led Schroeter to place the genus among the Rhizinaceae. The plant does, however, have a short stem and is more or less bulbous at the base. The lower margin of the hymenium is uneven, running down in points on the stem while naked strips extend upward for short distances into the hymenium as in some species of *Geoglossum.* There is a definite though inconspicuous margin to the hymenium and in dried plants the hymenium becomes reddish brown where the asci are numerous, while the stem remains whitish. The base of the plant is rounded like the base of species of *Morchella*. No thick mycelial root or sclerotium of any kind was found.

Sometimes the clubs are simple as shown on PLATE 2 and in Peck's illustration but they usually divide into fingers. The plant on PLATE 1 was divided near the middle. The halves have split and sprung apart as shown in *B*. The left branch shown at *A* is forked near the apex. The right branch was nearly destroyed by insects but appeared to have been more deeply divided. Other plants in the collections were divided a little below the middle. PLATE 2 shows two plants, one of which has been sectioned, closely caespitose and apparently connected at the base. In the cluster of small plants first discovered there were at least three connected at the base.

The whole interior of the plant—bulbous base, stem and ascoma—is perforated by irregular longitudinal cavities, as shown in the section on PLATE 2, *A*. The walls of the cavities are of nearly uniform thickness. The interior of the walls is composed of a mesh of septate hyphae 6–8μ in diameter. The cavities are lined with a palisade layer of regular, septate hyphae about 6μ in diameter. The layer is about 50μ thick and there are three or four septa in each hypha. The appearance of a cross section of one of the walls is like that shown in Hesse's Hypogaeen Deutschlands, *pl. 18*, *f. 12* (1894), except that the interior is composed entirely of septate hyphae.

The outside walls are covered with the hymenium on the outside and the palisade layer on the inside. The surface of the hymenium is wrinkled and corrugated, PLATE 2, *C*, but there appears to be no definite relation in position between the wrinkles of the hymenium and the internal cavities. The interior of the walls is composed of hyphae, and there appears to be no definite subhymenial layer. A palisade layer like that on the walls of the interior cavities covers the stem and base of the plant.

The asci, PLATE 2, *B*, are club-shaped, 10–12 × 160–200μ. They open by a lid as far as I can make out but I have not been able to find empty asci, which Boudier says must be examined to determine the nature of the opening. The character of the plant and the spores is that of Boudier's division Opercules. The paraphyses are septate, a little longer than the asci, slightly thickening upward and somewhat curved at the apex, 4–6μ in diameter.

The colors of the plant are whitish or cream colored outside and pure white within.

I have rewritten Peck's description to include the form of the base and method of branching, as follows:

Ascocarps single or caespitose, simple or more or less deeply and somewhat dichotomously divided, divisions columnar, straight or slightly curved, sulcate-costate and uneven; ascigerous layer definite but not separated from the short stem. Base even or slightly bulbous, interior perforated by irregular longitudinal cavities, separated by thin walls, whitish or brownish outside, pure white within, cavities lined with a regular palisade layer of septate hyphae; asci club-shaped, 10–12 × 160–200μ; paraphyses slightly longer than the asci, rarely branched, septate, 4–6μ in diameter; spores tuberculate, hyaline or slightly colored, elliptical, 10–13 × 18–24μ.

Varying greatly in size, 5–35 cm. high, 2–5 cm. thick.

Growing on the ground among grass or dead leaves in mixed woods.

Underwoodia columnaris is not closely related to any known discomycete. It forms a monotypic genus, as the term is usually understood. It appears to be the only representative of its group.

The group arrangement is especially applicable to the large discomycetes, for the groups are few and well marked; and, while the forms within them are closely related, the kinship of the groups themselves appears remote. Apart from *Underwoodia* there are only seven groups in the family Helvellaceae in our region: the *Morchella esculenta*, *Morchella hybrida* and *Verpa digitaliformis* groups in the *Morchella-Verpa* series and the *Gyromitra esculenta*, *Gyromitra infula*, *Helvella crispa* and *Helvella elastica* groups in the *Gyromitra-Helvella* series. In the Geoglossaceae there may be about thirteen groups, nine of which are in the large *Geoglossum* series and one each in *Spathularia*, *Cudonia*, *Leotia* and *Vibrissea*. The groups are also few and well defined among the larger Pezizaceae. The order Helvellales is based on little more natural relationship than that its members are the large conspicuously stemmed discomycetes.

Forms within the groups offer a most fruitful field for ecological and comparative study. Most of the groups of large discomycetes, such as the *Verpa*, *Cudonia*, *Leotia*, and *Geoglossum glutinosum* groups, appear in a variety of forms. In some groups the forms are very abundant and variable. Boudier has named and given beautiful illustrations of twenty-three forms in the *Morchella esculenta* group, offering a fine opportunity for students to compare other *Morchella esculenta* floras with that of France. Durand lists seven forms in the *Geoglossum glabrum* group. *Underwoodia* is so rare that its variation is little known, though it may have had a bloom period at some time in the past.

But while the kinship and variation of *Underwoodia* are unknown it possesses a striking combination of characters found singly in other groups. Most of these characters are more highly developed than in other groups where they occur and this gives to *Underwoodia* a unique position and a special interest. I can only briefly compare the most striking characters and do it without implying any close kinship between *Underwoodia* and the groups in which similar characters are found.

The cancellated stem of *Underwoodia* is more highly developed than in any other discomycete. It contrasts strongly with the hollow stems of species of *Morchella* and the solid stems of the Geoglossaceae. The character is found in the *Acetabula vulgaris* and the *Helvella crispa* groups, but the stems in these groups are deeply sulcate as well as cancellate, the cavities are much less regular and the walls of the cavities as far as I have examined them are not covered with a regular palisade layer. The stems of species of *Morchella* often have a few cavities near the base. They are very markedly developed in the specimen of *Gyromitra gigas* illustrated by Boudier (Icon. Mycol. *pl. 221.* 1904). Such cavities are not lined with a palisade layer of hyphae.

Many discomycetes have lacunae and cavities in the stem. An interesting case for comparison with *Underwoodia* was identified for me by Durand as *Lachnea* (or *Macropodia*) *semitosta.* The stem bears a close resemblance to that of *Underwoodia.* There are a few sulcations on the outside, but the walls of the cavities are not lined with such a regular palisade layer. *Macropodia semitosta* is remarkable in the development of the cancellated stem. Note the illustration of *Peziza semitosta* in Cooke's Mycographia, *f. 109* (1879). The palisade layer lining the cavities in the body of the fungus is most highly developed in species of Hypogaei, but in them it is connected with the hymenium. Bucholtz derives the Helvellaceae from *Lachnea* through the Hypogaei.

The cancellated stem is combined in *Underwoodia* with a club-shaped ascoma, not cup-shaped or saddle-shaped as in the *Acetabula* and *Helvella* groups. Such club-shaped ascomata are found in the groups of the *Geoglossum* series. In size, however, in substance, in the spores, and probably in the opening of the asci *Underwoodia* is widely removed from any of the groups in that series. The hymenium is also more sulcate than in species of *Geoglossum* and resembles in this respect the hymenium of *Verpa*. Compare Boudier's illustrations on *pl. 219* and *220*. We may also compare the ascoma of *Gyromitra gigas* referred to above. *Gyromitra gigas*, as illustrated by Boudier in *pl. 221*, is nearer in general shape and appearance to *Underwoodia* than any other discomycete with which I am familiar.

The spores of *Underwoodia* have a tuberculate wall and in this respect are more highly developed than is usual among the Helvellaceae, the other species of which have smooth, hyaline spores.

The question whether *Underwoodia* is a gymnocarp or an angiocarp cannot be settled without the young stages. In the ascoma of the species of *Helvella* the young hymenium is overgrown by surrounding tissue as in very many cup fungi and the same is true of the elements of the compound hymenium of *Morchella*. The hymenium of *Underwoodia* does not appear to have been so overgrown at any time, but whether it was covered at any stage with a weft of fibers, as is the case with many of the Geoglossaceae is not known. Nor is it known whether the hymenium originated on or below the surface of the primitive ascocarp. Questions as to the protection of the young hymenium in the discomycetes are not yet settled.

The high development of the different characters in *Underwoodia* gives it a most important position. It is one of the largest and certainly the most highly developed of all the discomycetes.

2. PUSTULARIA GIGANTEA Rehm

In July, 1899, I found some large cup fungi on the ground among dead leaves on Mackinac Island, Michigan. Later I sent them to Dr. H. Rehm, who described them as a new species under the name *Pustularia gigantea*. The description was published in Annales Mycologici (3: 517. 1915). I have since found the plant several times in coniferous woods on Neebish Island. In September, 1907, it was abundant in a piece of cedar and balsam woods, and I secured the photograph of the opened plant, PLATE 3, A, and preserved a number of unopened plants in alcohol, from which the photograph of the section, B, was made. The specimens sent to Dr. Rehm were dried and somewhat torn, so that they did not show the peculiar folding in of the edges of the apothecium and the way in which the mature plants burst open, which are two of the most striking characters of the species.

The unopened apothecia are irregularly ellipsoid with a deep groove across the top. The apothecia often occur in clusters in which the orientation of the members is irregular. The surface of the apothecia is nearly smooth, whitish in color, and much soiled by the earth or mould in which the plants are buried.

The apothecia have a definite interior structure which is shown in PLATE 3, B. This figure represents a vertical section cut from the center of an unopened apothecium. There is no stem and the flat under surface lies directly on the soil, with which it is connected by strands of white mycelium. Quite frequently the connection with the substratum is lost, as is the case with the Hypogaei.

The cup is roughly and partially divided into two chambers by the infolding of the edges of the apothecium. The chambers can be recognized in all the plants examined, though they are at times more or less distorted. The infolded edges extend to the bottom of the cup. In a section like this made through the center of the apothecium the infolded walls are divided at the base. In sections near the ends of the apothecium they are united. The walls have been infolded till the usual apical opening or mouth of the cup in other Pezizaceae lies on the bottom of the cup. Neither the lips nor the walls are grown together, though they are pressed closely against each other. In the section before us the walls have sprung apart. The lips are like those of other cup fungi with the hypothecium extending a little beyond and embracing the hymenium. The bottom of the cup is thickened and raised into a sort of cushion covered like the rest of the interior by the hymenium. Such a cushion is evident on the bottom of all the cups examined. Around the cushion is a narrow zone which is destitute of hymenium. It has apparently resulted from a rupture of the hymenium during growth. In the larger chamber is an irregular outgrowth covered by the hymenium such as may occur in almost any position on the hymenium of these plants.

An end section of another specimen shows an apothecium in which the basal cushion is very large. The chambers are irregular and there are several minor cavities. The general structure is however the same as in the plant figured on PLATE 3. The basal cushion in this second specimen is hollow and it was deeply indented on the under side in a zone around the central portion, which was attached to the soil as a sort of stem.

When the apothecia are mature and the growth tension becomes great; instead of opening at the mouth as in most species of *Peziza*, the walls of the chambers burst irregularly as shown in PLATE 3, *A*. The appearance of such opened plants is striking. The walls of the internal cavities are pure bluish white and the thick reflexed segments give the plant the appearance of a large white flower. When the weather is unfavorable to rapid growth the apothecia do not open as far as my observation goes but dry up or decay without exposing the hymenium. Sometimes irregular openings are found in the walls of old plants.

In regular plants the walls of the apothecia are of nearly equal thickness throughout. They are covered on the inside by the hymenium. The hypothecium is made up of irregular septate hyphae of different diameters with many large irregular cells and cavities, especially in the center. The hyphae are much more dense directly beneath the hymenium where they form an indefinite subhymenial layer. On the outside there is a compact cortical layer of hyphae which run somewhat parallel to the surface. In the center of the walls the tissue is looser and the cells larger. Often the tissue breaks down and leaves hollow spaces in the walls. as can be seen in the sections.

The asci are long and narrow and closely packed together with relatively few paraphyses. They measure 10–12 × 200–300μ. They are linear for most of their length, rounded-truncate at the apex and narrowed near the base. The base is enlarged and irregular. The paraphyses are about 2μ in diameter, slightly enlarged at the upper end, rarely branched and with few septa. The spores are oblong with rounded ends, smooth, usually with two oil drops when mature, 5–8 × 10–14μ.

Rehm placed the plant in the genus *Pustularia* and compared it with *Pustularia vesiculosa*, noting that it differed from that species in the larger size and smaller spores. According to Rehm's key *Pustularia* contains species of fleshy Pezizaceae, which have smooth and entire cups, asci turning blue with iodine, elliptical spores and sessile apothecia. It includes species like *Peziza vesiculosa*, *P. Stevensoniana*, and *P. coronaria*. Boudier disregards the surface of the apothecia and places species like *Peziza coronaria* and *Sepultaria sepulta* in a genus *Sarcosphaera*, on the ground that they are semi-subterranean with the apothecia closed at first and bursting irregularly at maturity. *Pustularia gigantea* is semi-subterranean in its habit and bursts irregularly at maturity and might be placed in this genus, but it has a definite mouth the walls of which have simply become infolded during growth.

The natural arrangement of the species of Pezizaceae has not yet been discovered. All that was said about the groups of the Helvellaceae above applies equally to the groups of the large cup fungi. As Dodge has emphasized, a knowledge of the early stages is a necessary prerequisite of a natural classification.

It is not certain to which group *Pustularia gigantea* belongs. It is not close to *Pustularia vesiculosa*, as Rehm suggests, for in addition to the difference in the size of the spores the subterranean habit and character of the mouth are very different from that species. Our collections of *Pustularia vesiculosa* have mouths of the ordinary form and grow in the mulching about trees and on manure heaps. They agree with Lloyd's photograph in Hard's Mushroom, *f. 432* (1908). *Pustularia gigantea* appears to be closer to *Peziza coronaria*, for that species is subterranean. Boudier's illustration, *pl. 302*, resembles our expanded plant. Cooke's illustration in Mycographia, *f. 238*, agrees in size and method of opening, and the same is true of Kalchbrenner's illustration of *Peziza coro-*

naria var. *macrocalyx* (Icon. Select. *pl. 40, f. 2*). The spores also are nearer in size to those of *Peziza coronaria* than to those of *P. vesiculosa*. Saccardo's Sylloge (8: 81. 1889) gives the spores of *P. coronaria* 8–9 × 15–18μ. The spores of *Pustularia gigantea* are often 8 × 14μ, though Rehm gives 5–6 × 10–12μ. The descriptions of *Peziza coronaria* do not, however, give the internal structure of the unopened apothecia. It is supposed that the young plants have no evident mouths. The species of *Sepultaria* also are said to be closed at first and to open irregularly. Yet what is known of the structure of the cup fungi suggests that in all these forms the hymenium has been overgrown by surrounding tissue, and the location of the mouth should be determinable even in young unopened apothecia. *Pustularia gigantea* is very enlightening on this point and the unopened apothecia of species like *Peziza coronaria* should be carefully examined to see if there is not evidence of the location of the mouth. It is uncertain whether *Pustularia gigantea* should be associated with *Peziza coronaria* or placed in a group by itself. Further observation may bring to light other more closely related forms.

The most striking feature of *Pustularia gigantea* is the degree in which the walls of the apothecia are infolded. It is very common among the discomycetes for the hymenium to be covered by the surrounding tissue during the formative period. In small species of *Peziza* the ascoma usually remains circular, but in large plants the walls of the cup are flattened and folded together from the sides. This is also true of species of *Helvella* which have a cup-shaped or saddle-shaped ascoma. The saddle-shaped ascoma in the *Helvella elastica* group is folded and flattened in the same way when young and later opens at the ends instead of in the middle giving it the characteristic saddle-shaped form.

Bucholtz has shown that in many of the Tuberaceae the hymenium is formed on the outside of the ascocarp and then overgrown by surrounding tissue until it is entirely enclosed in cavities of the fruit body. *Pustularia gigantea* has many characters in common with the Tuberaceae. The closed chambers, subterranean habit and loose connection with the soil are all suggestive of the Tuberaceae. We need only mention the Hysteriaceae to show how common the inrolling of the disk and consequent covering of the hymenium is among the discomycetes and their allies. The striking feature of *Pustularia gigantea* is the extent to which the walls are infolded The mouth is completely inverted and lies on the bottom of the cup. In this the plant appears to be unique.

Explanation of plates 1-3

PLATE 1. UNDERWOODIA COLUMNARIS Peck

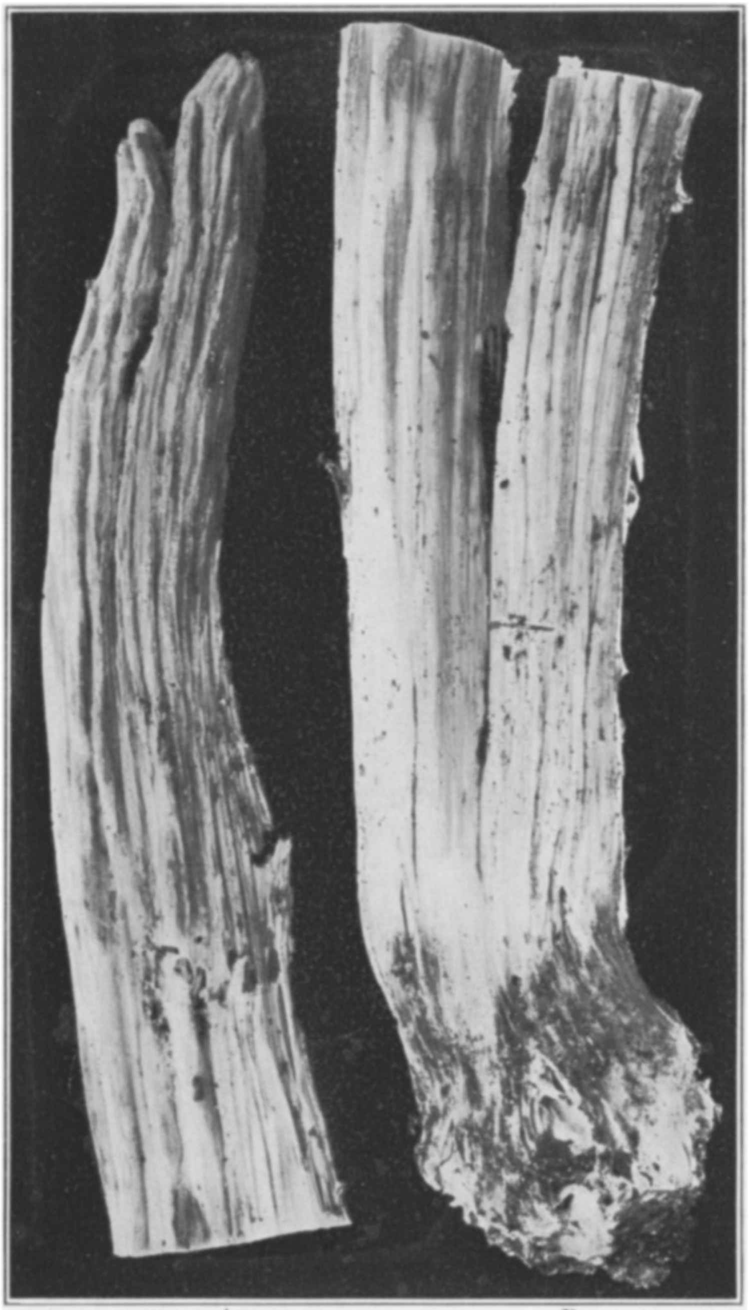
A, upper half of the left branch of a large plant; *B*, lower half of the plant.

PLATE 2. UNDERWOODIA COLUMNARIS Peck

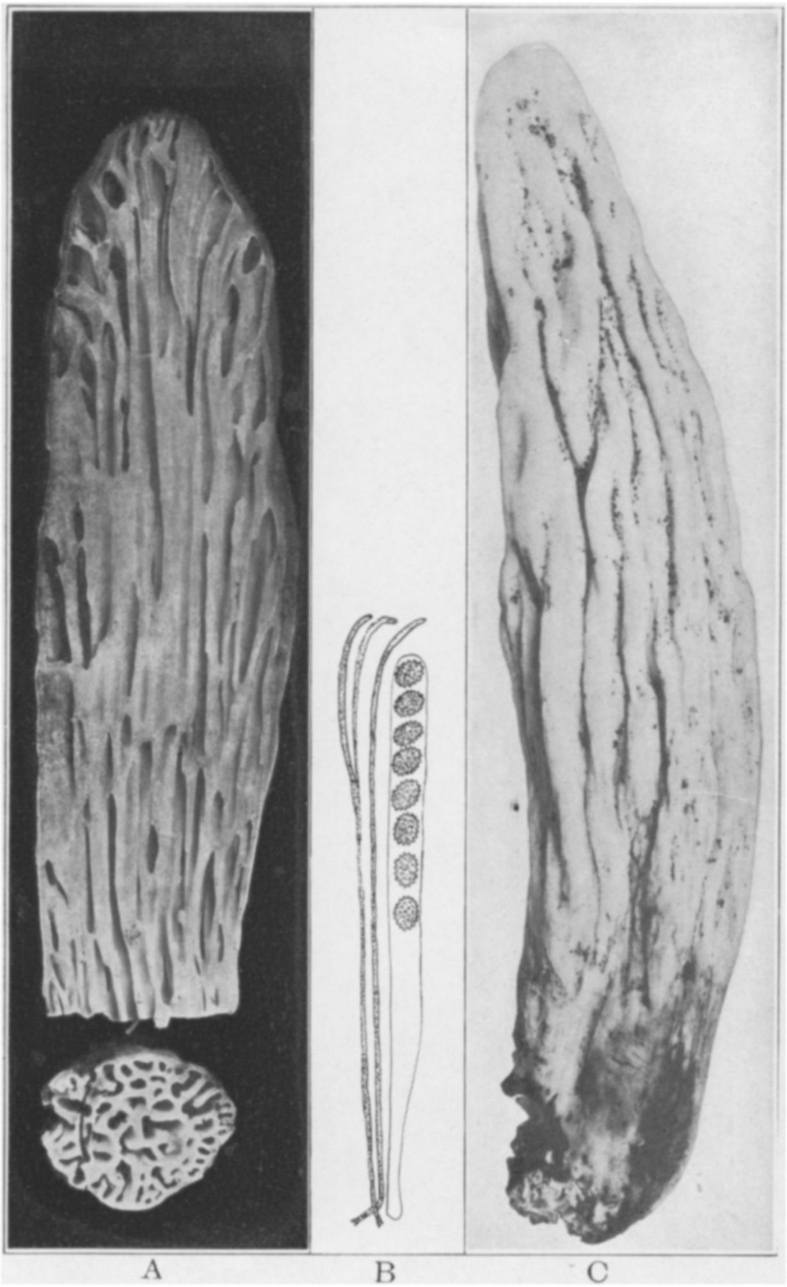
A, longitudinal and cross sections; *B*, ascus and paraphyses; *C*, one of a pair of plants grown together at the base.

PLATE 3. PUSTULARIA GIGANTEA Rehm

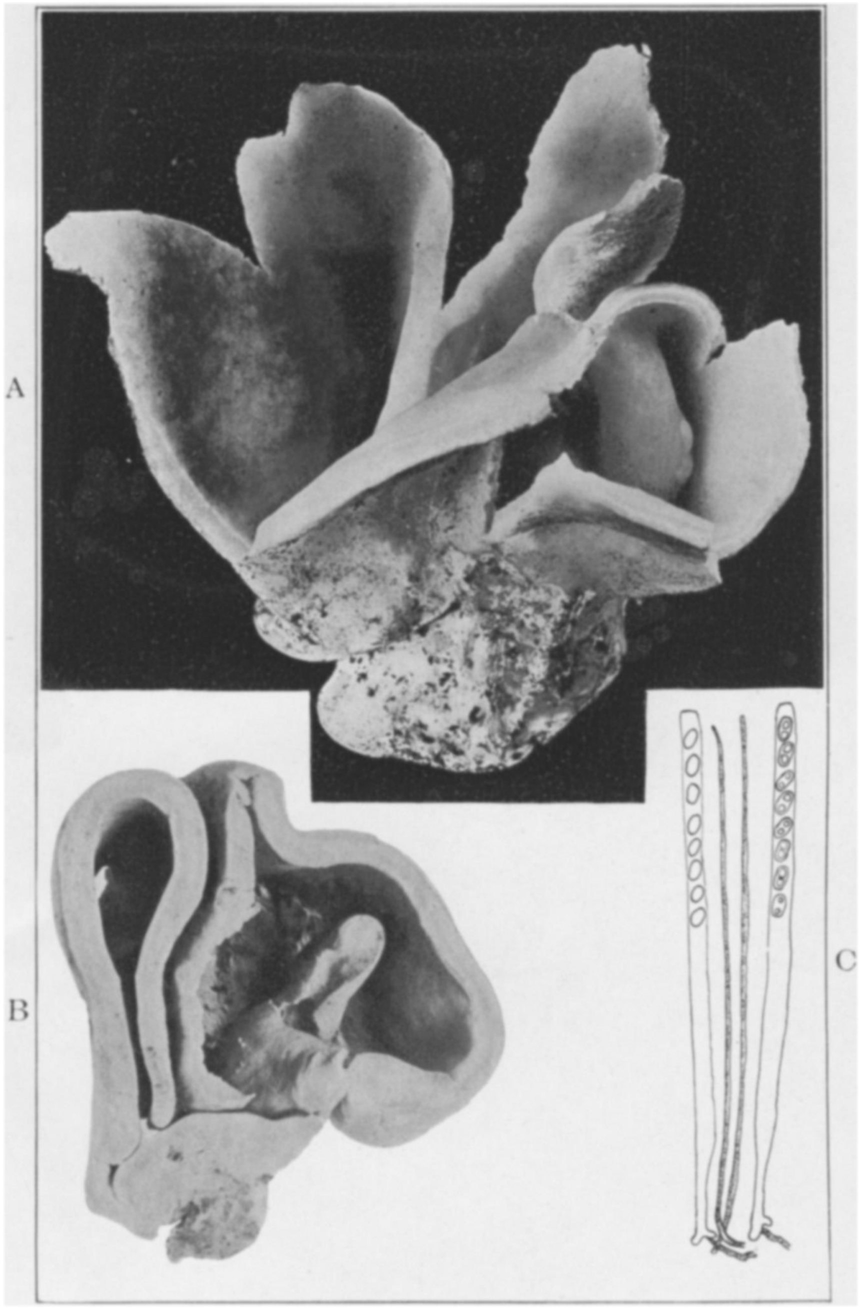
A, expanded plant. *B*, vertical section through an unopened apothecium; *C*, asci and paraphyses.



UNDERWOODIA COLUMNARIS Peck



UNDERWOODIA COLUMNARIS Peck



PUSTULARIA GIGANTEA REHM